Levels of Genetic Variation in Trees: Influence of life history characteristics[1]

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Abstract: In a previous study, levels of genetic variation, as measured by isozyme analyses, were compared for 113 taxa of vascular plants. Each species was classified for 12 life history and ecological traits and three measures of genetic variation were calculated. Plants with large ranges, high fecundities, an outcrossing mode of reproduction, wind pollination, a long generation time, and from habitats representing later stages of succession tended to have more isozyme variation than species with other combinations of characteristics. This paper discusses the results of the previous study and examines the available isozyme data for similar trends in forest trees. Special consideration was given to differences in genetic variation among 20 conifer species that have many of their life history characteristics in common. Successional stage, habitat type, cone type and historical events were associated with differences in genetic variation among the conifer species. These results are discussed in terms of expectations from current population genetics theory.

Forest trees have been the subject of many quantitative genetic investigations (Libby and others 1969, Stern and Roche 1974). These studies have concentrated on morphometric and physiological characteristics such as survival, growth initiation, height and diameter growth, hardiness to environmental stress, and various leaf, stem, fruit, and wood characteristics. As a result, the distribution of quantitative genetic variation is better understood in certain tree species than in most other naturally occurring plants.

Studies that use biochemical techniques to measure genetic variation in forest trees generally have lagged behind those that use quantitative traits. A few workers have used secondary plant compounds, such as terpenes, in studies of species (Zavarin and Snajberk 1969, Zavarin and others 1969), racial (Smith and others 1969) and population (Adams 1975a, 1975b) differentiation. But, because the genetic basis of variation in these compounds is poorly understood, they are of limited use in population genetic studies. Since the early 1970's, electrophoretic techniques have been used in genetic studies of forest tree populations. These techniques offer a number of advantages over other biochemical or quantitative approaches: (a) genetic inheritance of electrophoreticaIly-detectable traits can be easily demonstrated; (b) most isozyme loci are codominant and gene frequencies can be calculated without the necessity of genetic crosses; (c) estimates of genetic variation can be compared directly between populations or between species. The relatively few isozyme studies of plant populations have been the subject of a number of recent reviews (Gottlieb 1977, Brown 1979, Hamrick 1979, Hamrick and others 1979). Generally, these reviews have concluded that plants contain somewhat more variation than invertebrate animals and considerably more variation than most vertebrates. Furthermore, different plant species contain varying amounts of genetic variation. Trees, for example, have been found to contain significantly more variation than herbaceous plants (Hamrick 1979, Hamrick and others 1979).

This paper reviews the results of a previous study (Hamrick and others 1979), which compared the isozyme variation of plant species with different combinations of life history traits and examines the available isozyme data for similar trends in forest trees. Specifically, we address the following questions:

- Do plant species with certain combinations of life history traits contain higher levels of genetic variation?
- Does being a woody plant directly affect levels of isozyme variation?
- Can differences in genetic variation among tree species be explained by their life history and ecological characteristics?
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PROCEDURES

In a previous study (Hamrick and others 1979), we examined the relationship between 12 life history and ecological traits and the levels of genetic variation maintained within populations of 113 taxa of plants. Each species was classified for taxonomic status, geographic range, generation length, mode of reproduction, mating system, pollination mechanism, fecundity, seed dispersal mechanism, chromosome number, successional stage, habitat type, and cultivation status. Where the data allowed, three measures of intrapopulation genetic variation were calculated for each species: the percent of polymorphic loci per population (*P*), the mean number of alleles per locus (*A*), and a polymorphic index (*PI*). The *PI*

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Table 1—*Levels of variability among categories of 12 life history and ecological traits. Weighted means and standard errors are given for each measure of variability. Differences in* PI *between categories are tested by ANOVA. Statistical significance levels are given in parentheses (from Hamrick and others 1979)*

Variable	Species	Loci	Polymorphic loci (*P*)		Alleles per locus (*A*)		Polymorphic Index (*PI*)	
			$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
			Percent					
Taxonomic status							(P <0.01)	
Gymnospermae	11	9.2	67.01	7.99	2.12	0.20	0.270	0.041
Dicotyledoneae	74	11.4	31.28	3.31	1.46	.06	.113	.014
Monocotyledoneae	28	11.6	39.70	6.02	2.11	.19	.165	.026
Geographic range							(P < 0.05)	
Endemic	17	15.1	23.52	5.06	1.43	0.11	0.086	0.019
Narrow	22	11.4	36.73	6.01	1.60	.14	.158	.030
Regional	39	8.3	55.96	5.13	1.85	.10	.185	.025
Widespread	35	12.5	30.36	5.03	1.58	.15	.120	.021
Generation length							(P <0.001)	
Annual	42	11.2	39.47	4.32	1.72	0.11	0.132	0.017
Biennial	13	17.2	15.78	5.12	1.26	.09	.060	.020
Short-lived perennial	31	12.0	28.09	5.06	1.46	.09	.123	.023
Long-lived perennial	27	7.6	65.77	5.08	2.07	0.13	0.267	0.027
Mode of reproduction							N.S.	
Asexual	1	8.0	50.00	0.00	1.91	0.00	0.139	0.000
Sexual	95	11.7	35.64	3.03	1.63	.07	.135	.012
Both	17	8.9	41.71	8.12	1.67	.14	.185	.034
Mating system							(P < 0.01)	
Primarily selfed	33	14.2	17.92	3.21	1.27	0.06	0.058	0.014
Mixed	42	8.6	14.16	4.89	1.76	.10	.181	.022
Primarily outcrossed	36	11.3	51.07	4.95	1.85	.12	.185	.022
Pollination mechanism							(P <0.001)	
Selfed	33	14.2	18.99	3.51	1.31	0.07	0.058	0.028
Animal	55	9.5	38.83	3.94	1.55	.07	.130	.015
Wind	23	10.7	57.45	6.29	2.27	.17	.264	.028
Fecundity							(P < 0.001)	
$<10^2$	21	12.0	40.06	6.45	1.72	0.16	0.127	0.026
10^2 to 10^3	27	12.4	26.35	3.46	1.44	.07	.096	.013
10^3 to 10^4	22	11.9	36.98	6.37	1.64	.10	.199	.034
$>10^4$	40	9.8	67.99	5.99	2.27	.17	.286	.033
Seed dispersal mechanism							N.S.	
Large	27	11.4	37.42	3.73	1.76	0.156	0.0230	.16
Animal-attached	16	11.1	28.79	5.55	1.55	.08	.092	.020
Small	26	12.4	32.98	5.10	1.51	.09	.118	.018
Winged or plumose	21	12.2	44.91	7.27	1.86	.13	.188	.029
Animal ingested	20	7.0	32.98	8.25	1.43	.10	.132	.036
Chromosome number							(P<0.01)	
10 to 20	50	13.1	35.52	3.61	1.55	0.08	0.111	0.014
22 to 30	44	10.0	37.41	5.35	1.73	.10	.175	.023
>30	16	8.9	41.65	7.20	2.10	.14	.224	.030
Stage of succession							(P <0.01)	
Weedy and early	54	12.5	29.67	3.82	1.60	0.08	0.116	0.015
Middle	49	9.7	37.90	4.43	1.56	.08	.137	.019
Late	10	12.0	62.76	5.28	2.14	.19	.271	.038
Habitat type							N.S.	
Xeric	4	8.8	15.39	8.20	1.11	0.09	0.048	0.040
Submesic	19	10.5	43.68	4.86	1.66	.08	.140	.020
Mesic	82	11.4	36.01	3.61	1.65	.07	.146	.016
Hydric	8	13.0	27.71	10.33	1.59	.22	.145	.050
Cultivation status							N.S.	
Cultivated	21	6.8	38.99	7.15	1.61	0.12	0.172	0.032
Noncultivated	89	12.6	36.10	3.12	1.63	.07	.136	.013
Both	3	2.7	50.00	—	1.75	.21	.209	.035

is equivalent to the Hardy-Weinberg heterozygosity (Hamrick and Allard 1972).

For each category of the 12 life history variables weighted (by the number of loci), means were calculated for *P, A,* and *PI,* and mean *PI* values were compared for heterogeneity by single classification ANOVA. Multivariate statistics were used to determine correlations among traits and to test whether combinations-of life history variables influence genetic variation. The data were analyzed first with a principal components analysis to describe the major patterns of covariation. Associations noted in this analysis were explored further with a stepwise multiple regression.

Differences in genetic variation among tree species was the subject of a second analysis. This analysis included studies not available earlier but was limited to studies that used a wide variety of enzyme systems. Values of *P, A,* and *PI* were calculated for each species and weighted means were calculated for each category of six variables. Multivariate analyses were not used since most of the tree species were conifers and, therefore, similar for many of their life history traits.

RESULTS

Isozyme Variation in Plants

The mean values of *P, A,* and *PI* obtained by pooling the 113 taxa in our original study were: *P*= 36.8 percent, *A* = 1.69, and *PI* = 0.141. When compared with animals, plants tend to have levels of genetic variation that are roughly equivalent to the invertebrates (*P*= 46.9 percent, *PI*= 0.135 [Selander 1976]; *P* = 39.7 percent, *PI* = 0.112 [Nevo 1978]) but are considerably higher than those of vertebrate species *(P* = 24.7 percent, *PI* = 0.061 [Selander 1976], *P* = 17.3 percent, *PI* = 0.036 [Nevo 1978]).

Genetic Variation and Life History Traits

Statistically significant differences (P<0.05) were found among categories of eight life history or ecological traits (*table 1*). Gymnosperm species tended to have more variation than angiosperms while regionally distributed species had more variation than those with other geographic ranges. We had expected species with the widest ranges to contain the most variation. Many species in this category, however, are weedy or early successional species that tend to have less variation. Long-lived perennials and plants with mixed or primarily outcrossed mating systems contained at least twice the variation of species in other categories. Within the outcrossed species, wind-pollinated species had more variation than those with animal pollination. Species with high fecundities and high chromosome numbers also had more variation as did species of the later stages of succession.

Multivariate techniques were used to identify groups of variables varying in concert, and to assess the covariation of genetic variation with ecological and life history variables. Approximately one-half of the correlations among the ecological, life history, and genetic variables were statistically significant. Pollination mechanism, mating system, and fecundity had the highest correlations with the genetic variables. Additional multivariate analyses demonstrated that only the first two principal components contributed to our understanding of the genetic variation among these species. The first principal component, which had high loadings from the three genetic variables, generation length, mating system, pollination mechanism, fecundity, seed dispersal and successional status explained 30 percent of the variation. The second principal component, which had high loadings from the genetic variables, taxonomic status, seed dispersal mechanisms, and successional stage explained 16 percent of the variation. These results were consistent with the univariate analyses and indicated that species with large ranges, high fecundities, an outcrossing mode of reproduction, wind pollination, a long generation time, and from habitats representing later stages of succession had more genetic variation than did species with other combinations of traits. It is worth noting that forest trees in general and conifers in particular combine many of the characteristics that are associated with high levels of genetic variation.

To determine which ecological and life history traits were most closely associated with genetic variation we employed a stepwise multiple regression analysis in which *PI* was the dependent variable and the 12 ecological and life history traits were independent variables. Only two variables were significant—pollination mechanism and fecundity. Species that are wind pollinated and highly fecund were the most genetically variable.

Variation Among Tree Species

The separate analyses of the tree data produced some noteworthy results. First, the mean level of variation within populations of coniferous trees was lower than that reported previously (Hamrick and others 1979). In the earlier review (Hamrick and others 1979), the inclusion of studies based solely on polymorphic loci tended to increase estimates of the mean levels of variation. Also, many of the earlier tree studies used enzyme systems such as esterases and peroxidases that are often highly variable. The data in the present analyses are relatively free of these biases and should be more representative of the actual levels of genetic variation in tree populations. It is significant, therefore, that the mean levels of variation in tree populations continue to exceed that of herbaceous species by more than 60 percent.

A second important result is the continued observation of interspecific differences in genetic variation. The *PI* varies from 0.000 for red pine (*Pinus resinosa* Ait.) to 0.364

Table 2—*Summary of electrophoretic studies of genetic variation in trees. P = percent of polymorphic loci, A = alleles per locus, PI = polymorphic index*

Species[1]	Location	Loci	Populations	*P*	*A*	*PI*	Source
			A. Gymnosperms				
Abies balsamea	New Hampshire	14	1	64.0	1.86	0.150	Neale (1978)
Picea abies	Sweden	12	4	91.7	3.54	.341	Lundkvist (1979)
P. sitchensis	Rangewide	24	10	—	1.90	.150	Yeh, F. (unpubl.)
Pinus aristata	Rangewide	22	5	46.4	1.55	.139	Hiebert, R.D. and Hamrick, J.L. (unpubl.)
P. attenuata	Rangewide	22	10	73.0	2.09	.140	Conkle, M.T. (unpubl.)
P. balfouriana	Rangewide	23	4	57.6	1.61	.208	Hiebert, R.D. and Hamrick, J.L. (Unpubl.)
P. banksiana	Michigan	21	1	28.6	—	.083	Snyder, T. (unpubl.)
P. contorta	British Columbia	27	17	—	1.90	.150	Yeh, F. (unpubl.)
P. contorta	California	37	1	89.2	2.78	.190	Conkle, M.T. (unpubl.)
P. contorta	Colorado	26	1	42.0	1.42	.160	Hamrick, J.L. (unpubl.)
P. lambertiana	Rangewide	20	—	80.0	2.85	.260	Conkle, M.T. (unpubl.)
P. longaeva	Rangewide	14	5	78.6	2.35	.364	Hiebert (1977)
P. jeffreyi	California	44	1	—	2.90	.260	Conkle, M.T. (unpubl.)
P. muricata	Northern California	17	1	65.0	1.53	.090	Millar, C. (unpubl.)
P. ponderosa	Eastern Colorado	22	7	68.4	2.00	.226	Hamrick, J.L. (unpubl)
P. pungens	Rangewide	15	3	40.0	1.33	.144	Feret (1974)
P. resinosa	Rangewide	9	5	0.0	1.00	.000	Fowler and Morris (1977)
P. rigida	Rangewide	21	11	78.8	2.19	.144	Guries, R. and Ledig, T. (unpubl.)
P. strobus	Seed Orchard, New Hampshire	17	—	52.9	2.06	.330	Eckert and others (1980)
P. taeda	North Carolina	11	1	100.0	3.73	.340	Conkle, M.T. (unpubl.)
P. taeda	Superior Trees	30	—	93.3	3.87	.260	Conkle, M.T. (unpubl.)
P. taeda	Seed Orchard, South Carolina	15	—	80.0	2.93	.200	Adams and Joly[2]
Pseudotsuga menziesii	British Columbia, Interior	21	11	—	2.23	.180	Yeh, F. (unpubl.)
P. menziesii	Coastal	21	11	—	2.23	.150	Yeh, F. (unpubl.)
P. menziesii	California Coastal	11	9	74.2	3.17	.332	Morris, R. (unpubl.)
P. menziesii	California Interior	17	1	100.0	1.78	.330	Conkle, M.T. (unpubl.)
P. menziesii	Eastern Colorado	22	5	64.0	1.86	.264	Hamrick, J.L. (unpubl.)
Sequoiadendron giganteum	Rangewide	8	34	50.0	2.63	.155	Fins, L. (unpubl.)
	Mean	20.1		67.7 ±4.9	2.29 ±0.14	.207 ±.017	
			B. Angiosperms				
Persea americana cultivars		10		80.0	1.90	.195	Torres and others (1978)
Phoenix dactylifera cultivars		7		100.0	2.00	.332	Torres, A.M. (unpubl.)
	Mean	8.5		88.23 ±10.0	1.94 ±0.05	.251 ±.028	

[1]Only those studies that used a variety of enzyme systems are included.
[2]Adams, W.T., and R.J. Joly. Allozyme studies in loblolly pine seed orchards: clonal variation and frequency of progeny due to self-fertilization (Manuscript in preparation.)

for Great Basin bristlecone pine (*P. longaeva* D.K. Bailey). Since the 20 conifer species have many of their life history characteristics in common, only six traits were available to explain the differences in genetic variation observed among species—taxonomic status, geographic range, stage of succession, habitat type, cone type, and U.S. distribution.

The present data (*table 2*) are inadequate to determine whether differences between angiosperm and gymnosperm trees were significant. The two studies of angiosperm trees that met our criteria involved commercial cultivars of fruit trees. Although angiosperm trees appear to have as much genetic variation as conifers, final conclusions must await studies of naturally occurring angiosperm trees.

The geographic range of each conifer was classified as endemic, narrow, or regional *(table 3).* Most species had a regional distribution with only foxtail pine (*Pinus balfouriana* Grev. & Balf.) and giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) classified as endemics. The differences in *PI* between these categories were small and were not significant ($P < 0.50$).

The ability of a species to successfully reproduce in its own shade and in the absence of environmental disturbance was used to classify the species into one of

Table 3—*Levels of variability among categories of five life history and ecological variables for 28 conifer studies. Weighted means and standard errors are given. Differences in PI between categories are tested by ANO VA. Significance levels are indicated in parentheses*

Variable	Species[1]	Studies	Mean loci	Polymorphic Index (*PI*)	
				Mean	*S.E.*
Geographic range				($P < 0.50$)	
Endemic	2	2	15.5	0.194	0.052
Narrow	8	8	22.2	.197	.032
Regional	10	18	19.7	.207	.023
Stage of succession				($P <$ 0.10)	
Early	7	10	19.9	0.161	0.030
Middle	7	11	19.8	.241	.022
Late	7	7	20.8	.204	.035
Habitat type				($P <$ 0.10)	
Xeric	3	3	19.3	0.194	0.075
Submesic	11	15	21.7	.186	.021
Mesic	6	10	17.9	.238	.026
Cone type				($P <$ 0.01)	
Closed cone	6	7	21.3	0.132	0.012
Open cone	15	21	20.4	.226	.020
United States distribution				(P<0.30)	
Northeastern	5	5	16.4	0.152	0.054
Southern	2	4	17.8	.235	.042
Western	12	18	22.1	.204	.018

[1] Some species may be represented in more than one category.

three stages of succession (*table 3*). More variation ($P < 0.10$) was observed in populations of middle and late successional species and less in populations of pioneering species. Only the presence of loblolly pine (*P. taeda* L.) in the early category prevented the results from being statistically significant.

Differences among the habitat categories approached statistical significance ($P < 0.10$), but no definite trend can be seen (*table 3*). Differences between the submesic and mesic categories suggest a pattern but with only two species in the xeric category no definite conclusions can be drawn. Studies of genetic variation in conifer species that are adapted to drought conditions, such as the piñon pines and junipers, should yield valuable information on this question.

Species with closed cones or ecotypes of species that have closed cones were grouped together. These species had significantly less variation ($P<0.01$) than open-coned species (*table 3*).

Species which inhabit different geographic regions within the United States may also have different levels of genetic variation. The northeastern species (*Abies balsamea* [L.] Mill., *Pinus banksiana* Lamb., *P. resinosa* Ait., *P. rigida* Mill., and *P. strobus* L.) have somewhat less variation ($P < 0.30$) while the southern (*Pinus taeda* L. and *P. pugens* Lamb.) and the western species have higher values.

To summarize the results of the analyses on trees, species of later successional stages, mesic habitat types, with open cones and a southern or western distribution have more genetic variation than species with alternate combinations of characteristics.

DISCUSSION

A significant proportion of the differences in genetic variation among plant species is accounted for by variation in their life history and ecological characteristics. Species with large ranges, high fecundities, an outcrossing mode of reproduction, wind pollination, a long generation time and from habitats representing later stages of succession have higher amounts of genetic variation. This result is generally consistent with that predicted by population genetics theory. Plants, in general, might be expected to maintain high levels of genetic variation within their populations since their sessile nature often leads to the evolution of locally adapted ecotypes (Antonovics 1971, Bradshaw 1972, Jain and Bradshaw 1966). Also, long-lived plant species with large ranges and high fecundities typically have large, stable populations. Such populations are resistant to chance fluctuations in gene or genotype frequencies and should maintain more variation than populations that experience large fluctuations in size. Longevity also ensures the representation of many cohorts within a population. If different alleles or genotypes are favored during the establishment phase of each cohort, individuals that survive to maturity will maintain a genetic

"record" of these evolutionary events. Their continued survival would retard the loss of genetic variation. Greater longevity could be especially effective in maintaining genetic variation in later stages of succession because individuals are continuously becoming established in a highly complex biotic environment. It should be noted, however, that the seed carryover abilities of many annuals and short-lived perennials could produce a similar genetic record. Finally, high rates of fecundity, outcrossing and wind pollination ensure large neighborhood sizes and the production of a variety of genotypes through recombination. Natural selection could act to maintain this variation through the evolution of locally adapted ecotypes or through various types of balancing selection.

The existence of high levels of genetic variation in forest tree populations can be explained primarily by their life history and ecological characteristics. The question remains, however, of whether woodiness has a direct effect on the levels of genetic variation that are maintained. Current evidence, although scanty, indicates that herbaceous species with life history or ecological traits similar to those of trees also have high levels of genetic variation. This would argue against woodiness itself as affecting the maintenance of genetic variation. An alternate argument can be made on the basis of differences in life forms (Raunkiaer 1934) between woody and herbaceous plants (Hamrick 1979). Woody plants are phanerophytes and maintain their apical meristems above ground. Their apical meristems, therefore, are exposed to environmental fluctuations throughout the year. Herbaceous perennials are either chamaephytes, hemicryptophytes or cryptophytes whose apical meristems are located at or below the soil surface during periods of severe environmental stress. The moderating effects of snow, soil, or litter cover may, in essence, reduce selection pressures for the internal buffering thought to be produced by increased heterozygosity (Lerner 1954). If this argument is valid we would expect to find differences in genetic variation between populations of herbaceous and woody plants that occur in the same habitats and have similar life history traits. Also, we would expect to find an increase in heterozygosity in older age classes and in temporally fluctuating environments. An increase in heterozygosity in older age classes was demonstrated in a population of *Liatris cylindracea* Michx. (Schaal and Levin 1976). A further test of this argument would be provided by surveying a wider variety of woody trees and shrubs.

Differences in genetic variation among the conifer species surveyed are somewhat more difficult to explain. This is because the 20 conifer species have many of their life history characteristics in common. Although only one of the six traits — cone type — was statistically significant, geographic range was the only trait that failed to have large differences among the mean *PI* values. This result is not surprising since endemic and narrowly distributed tree species often have rather large population sizes where they occur. Also both of the endemic species, *Pinus balfouriana* Grew. & Balf. and *Sequoiadendron giganteum* (Lindl.) Buchholz, are long-lived and could maintain genetic variation by this mechanism.

Trends observed for stage of succession, habitat type, and cone type in the conifer data are generally consistent with previous results (Hamrick and others 1979); conifers from mid- and late-successional stages, mesic habitats, and with open cones tend to have higher levels of genetic variation. Trees of early successional stages must adapt to relatively homogeneous environmental conditions that are influenced primarily by physical factors. Coupled with their colonizing habit, such uniform selection pressures might lead to a reduction in genetic variation. As succession proceeds, the biotic environment becomes increasingly important and, as a result, habitats become more complex and heterogeneous. Such complex environments may select for the maintenance of higher levels of genetic variation. A similar explanation may apply to the higher levels of variation observed in the more mesic adapted trees.

The lower levels of variation found in the closed-cone pines could result from a combination of factors. First, the closed-cone species are adapted to habitats which experience periodic catastrophic wildfires and are, therefore, almost always members of early successional communities. Such species germinate and grow under relatively uniform environmental conditions. Also, the closed cone habit and short life expectancy ensures even-aged stands. The genetic record of the long-lived, uneven aged species is not, therefore, an important factor in the maintenance of genetic variation in closed-cone species.

The geographic region to which conifer species are native also seems to affect genetic variation. Four of the five northeastern conifers maintain less variation than their southern and western counterparts. Two factors may help to explain this observation. First, it could be argued that western habitats are environmentally more heterogeneous than those in the northeast. Support for this argument comes from the greater diversity of community types in the West (Küchler 1964). The high variation in the two southern species contradicts this argument, however. A second factor to consider is the evolutionary history of each species. The northeastern species have been exposed to numerous continental glacial events. Glaciation may have greatly reduced the ranges of the northeastern species and reduced population sizes and genetic variation. Although the western species have also been exposed to changes in climatic factors and shifts in their ranges, the more varied topography of the West may have provided a greater variety of refugia. In fact, some of the western species expanded their ranges during glacial periods (for example, *Pinus longaeva* D. K. Bailey[4]).

In conclusion, a thorough knowledge of a species' life history and ecological characteristics is essential if its genetic structure is to be understood. Much of the heterogeneity in genetic variation seen among species can

[4]Personal communication from P.V. Wells,

be explained by such considerations. A significant amount of unexplained heterogeneity remains, however. Past historical events and characteristics which have not been considered may partially explain the differences that remain. As additional plant species are studied we should gain a clearer understanding of the role that life history characteristics, or combinations of characteristics, play in shaping the genetic structure of plant populations, including those of forest trees.

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